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Assessing opportunities to support coral reef climate change refugia in MPAs: A case study at the Revillagigedo Archipelago

Amber L. Carter [a,*], A. Meriwether W. Wilson [a], Maximiliano Bello [b,a], E. Mauricio Hoyos-Padilla [c], Mark E. Inall [a,d], James T. Ketchum [c], Andrew Schurer [a], Alexander W. Tudhope [a]

[a] School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FE, UK
[b] The Pew Charitable Trusts, 901 E Street NW, Washington, DC 20004-2008, USA
[c] Pelagios Kakunjá A.C., La Paz, Baja California Sur, Mexico
[d] SAMS/UHI, Scottish Marine Institute, Argyll PA37 1QA, UK

ABSTRACT

Coral reef refugia are habitats which possess physical, biological and ecological characteristics that make them likely to be relatively resilient to future climate change. Identification of refugia locations will be important to ensure suitable marine conservation planning is undertaken to protect sites where coral ecosystems will be better preserved now and in the future. This paper presents (1) a review of current knowledge of the oceanographic conditions and coral community in the Revillagigedo Archipelago Large Scale Marine Protected Area, (2) the first assessment of the potential for the Revillagigedo Archipelago to act as a climate refugia site for corals and coral reefs in the eastern tropical Pacific, and (3) consequent management and learning opportunities, to inform reef conservation both locally and globally. Through utilising published literature, remote and *in situ* environmental data, and field observations it was found that the Revillagigedo area exhibits a combination of distinctive characteristics in the coral community and in oceanographic processes which support conditions of refugia. The potential for refugia is further enhanced due to the absence of significant secondary anthropogenic stressors. This leads to a recommendation to establish the Revillagigedo as a globally significant 'sentinel site' where, through long-term monitoring of oceanographic conditions and of the coral and associated ecosystems, the effects of climate change can be quantified, and the effectiveness of specific refugia attributes established. This information may then be used to underpin the recognition of potential coral refugia elsewhere, and to guide MPA designation and management decisions to enhance their effectiveness.

1. Introduction

Coral reefs are among the most biodiverse ecosystems on Earth and have substantial global economic importance [1,2], yet it is widely recognised they are one of the ecosystems most vulnerable to climate change [3]. However, the extent to which corals are impacted by climate change will not be uniform, and some areas are expected to be less vulnerable than others [4].

1.1. Concept of coral climate refugia

The term 'refugia' refers to habitats with favourable environmental conditions that may offer safe havens for species under anthropogenic climate change [5]. The identification of refugia and its incorporation into conservation and spatial planning strategies may be instrumental in safeguarding the health and persistence of coral ecosystems in the future [6]. For example, recognition of refugia within new and existing marine protected areas (MPA) could contribute towards the recognition and protection of a 'climate-resilient' coral network [7].

Since the turn of the 21st century, there has been an increasing body of work defining the ecological and oceanographic conditions that characterise refugia for corals [8–11]. An essential component of refugia for corals is the long-term absence or reduction of stressful conditions [10]. Stressful conditions can cause the expulsion of symbiotic algae from the coral polyp, leading to coral bleaching and increased likelihood of coral mortality [12]. Recent mass coral bleaching events, caused by prolonged ocean temperature anomalies [13], demonstrate buffering against ocean warming will be a critical characteristic of refugia. Buffering against ocean acidification may also be essential, as decreasing pH and carbonate saturation in seawater inhibits the growth of the coral skeleton [14]. In addition, locations with buffering against threats such as sea level rise [15], changes in ocean circulation [16] and stratification [17], and increasing disease [18] are also likely to play an important role. Within such locations, the effectiveness of sites to serve as refugia

* Corresponding author.
E-mail address: amber.carter@ed.ac.uk (A.L. Carter).

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will be enhanced by the presence of conditions which promote coral resilience [10] and be influenced by the ecological and biogeographic characteristics of the coral community [11]. Resilience can occur though acclimatization of corals to unfavourable conditions and/or the selection of a more resistant coral host (or symbiont) following a disturbance event [19]. In particular, locations of high-frequency temperature variability have been identified as potential thermal refugia for corals as temperature fluctuations on daily timescales can promote tolerance to thermal stress and hence reduce the incidence of coral bleaching [20–22]. The maintenance of coral populations and recovery after disturbance events will be inherently linked to coral survival, the degree of self-recruitment and larval connectivity with other coral populations; however, the role of these processes is complex and will vary between locations [23]. In areas of potential refugia, absence of exposure to significant direct anthropogenic pressures will support the resilience of corals [24] and enable the maximum capacity of refugia to be attained [8].

1.2. Study overview

Here we present a review of the oceanographic conditions and reef coral community at the Revillagigedo Archipelago (Fig. 1) and discuss its potential to be a location of climate refugia for reef corals. The Revillagigedo Archipelago is a group of four isolated islands located in the Eastern Tropical Pacific (ETP) and is designated as a large-scale marine protected area (LSMPA). It hosts a diverse marine ecosystem and is recognised as a distinct ecoregion in the biogeographic province of the ETP [25]. The ETP is of interest for studies of coral climate refugia as reef building corals exist in conditions of exceptional environmental heterogeneity caused by complex currents [26], mesoscale upwelling [27] and a strong and shallow thermocline [28]. Moreover, across the region there is a spectrum of exposure to thermal stress related to the El Niño Southern Oscillation (ENSO) climate phenomenon, and to lowered carbonate saturations states associated with CO_2 outgassing [117]. In this study a characterisation of the oceanographic conditions and reef coral community at the Revillagigedo Archipelago is undertaken utilising a literature review, available remotely sensed sea surface temperature data, and new *in situ* temperature data. Owing to the isolated location of the Revillagigedo Archipelago, published descriptions of the coral community are infrequent and hence we supplement our review with unpublished observations based on some of the authors' extensive fieldwork in the region. Previously, the local oceanographic conditions at the archipelago have received little attention (only [30]) and therefore we undertake a detailed analysis of local high-frequency temperature variability detected by *in situ* temperature loggers. Finally, we discuss the findings from this review of oceanographic conditions and coral ecosystem in the context of climate refugia and discuss potential management implications for the Revillagigedo Archipelago LSMPA. Owing to the data available, this study focusses on thermal refugia, however, it is recognised that some coral reef settings will also need to function as refugia against multiple stressors, including ocean acidification and depleted oxygen.

2. Materials and methods

2.1. Literature review

A literature review was conducted to synthesise current knowledge

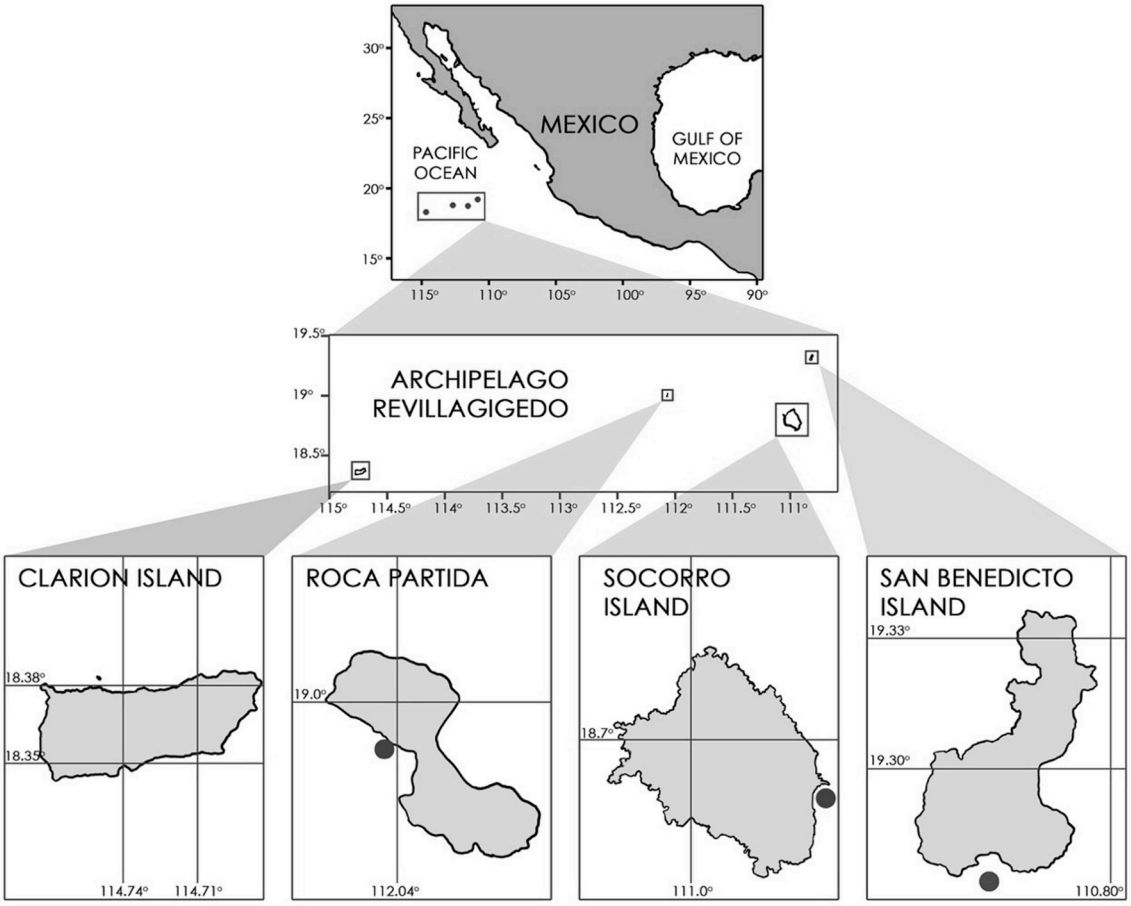

Fig. 1. Location of the Revillagigedo Archipelago in the eastern tropical Pacific and the location of HOBO temperature logger sites at Roca Partida, Socorro and San Benedicto islands. The maximum North-South dimensions of the islands are: Clarion ~3.7 km; Roca Partida ~0.1 km; Socorro ~16.4 km; San Benedicto ~4.1 km.

of the oceanographic conditions and coral community at the Revillagigedo Archipelago. The literature search was conducted using the electronic search database Web of Science. Specific studies of oceanographic and ecologic conditions at the Revillagigedo Archipelago are limited, and therefore, work from all years was considered. Publications in both English and Spanish were included.

2.2. Sources of existing data

Long term sea surface temperature (SST) data for the region of the Revillagigedo Archipelago (114.5°W-110.5°W and 18°N-20°N) was obtained from the Hadley Centre Sea Ice and Sea Surface Temperature data set (HADISST) [31] for the period of 1880–2016. Further SST and SST anomaly data was obtained from the Integrated Global Ocean Services System (IGOSS Reyn_Smith OIv2) [32]. Seasonal and monthly climatology measurements for thermocline depth data were obtained from NOAA World Ocean Atlas 2009 [33].

The influence of the El Niño Southern Oscillation (ENSO) on SST at the Revillagigedo Archipelago was analysed using linear regression between satellite-derived SST anomalies [32] measured for the 1° grid box containing each island and the Niño-3 Index (which is a commonly used measure for eastern Pacific El Niño events, and comprises SST anomalies averaged over the area 5° N–5° S, 150° W–90° W). Regression analysis was completed on SST anomaly measurements averaged over annual, seasonal and monthly timescales. Seasons were defined as December-January-February (boreal winter), March-April-May (boreal spring), June-July-August (boreal summer), and September-October-November (boreal autumn). The comparison was done for the period 1982–2016.

To investigate the potential impact of historic El Niño events on coral bleaching at the Revillagigedo Archipelago, NOAA degree heating weeks (DHW) methodology was used with IGOSS SST data for the 1° × 1° grid box containing each island. DHW is the cumulative measure of the intensity and magnitude of thermal stress from accumulated temperatures over a defined bleaching threshold in a 12-week period. In this methodology, the bleaching threshold is calculated as 1 °C above the maximum monthly mean temperature [34].

Historical cyclone paths were retrieved from https://coast.noaa.gov/hurricanes.

2.3. In situ temperature logger data and analysis

New, unpublished *in situ* ocean temperature data were utilised to investigate localised oceanographic conditions. These *in situ* temperature data were retrieved from three HOBO Water Temp Pro v2 loggers (deployed and maintained by Pelagios Kakunjá) located at the islands of San Benedicto, Socorro and Roca Partida at 23 m, 28 m and 38 m water depth, respectively. The loggers have a manufacturer's claimed temperature accuracy of±0.2 °C and resolution of±0.02 °C at 25 °C and a time accuracy 1 min/month (www.onsetcomp.com). The temperature loggers recorded data at 13-min intervals for 8 months at San Benedicto and Roca Partida between May 2016 and January 2017 and for 8.5 months at Socorro between June 2016 and March 2017. Power spectra of the temperature records was calculated with SSA-MTM Toolkit [35] using the Blackman and Tukey correlogram method.

3. A review of current knowledge and new observations on the oceanographic conditions and coral community at the Revillagigedo Archipelago

3.1. Research setting

The islands of the Revillagigedo Archipelago are located 350 km–650 km south and south west of the southern tip of the Baja California Peninsula in Mexico. The islands are uninhabited except for residents of naval bases on the two largest islands (Socorro and Clarion). Between November and May, a small number of licensed liveaboard dive boats operate in the area. Outside these months the islands are closed to tourism due to the regular occurrence of tropical cyclones. The marine ecosystems of the archipelago have been recognised for their abundance and diversity of large pelagic species including the presence of 36 species of elasmobranch [36] and an internationally significant aggregation site for giant manta rays (*Mobula birostris*). The islands are also an important breeding site for the silvertip shark (*Carcharhinus albimarginatus*) [37], the whitetip reef shark (*Triaenodon obesus*) [38], the Galapagos shark (*Carcharhinus galapagensis*) [38], the green sea turtle (*Chelonia mydas*) [39], humpback whales (*Megaptera novaeangliae*) [40] and several species of seabird [41]. The Revillagigedo Archipelago hosts a diverse reef ecosystem with 251 species of reef fish recorded [36] and a relatively species rich coral community for the biogeographic region of the ETP [42]. Trophic interactions between the pelagic and reef ecosystems at the archipelago have not been well studied, however, the presence of reef fish-megafauna cleaning stations and complex ocean-island trophic food webs [43] indicate there could be significant interactions between the pelagic and reef ecosystems [44]. Since 2016 the islands and surrounding marine areas have been listed as a UNESCO World Heritage Site, and in 2017 an ocean region of 148,800 km^2 around the archipelago was designated as an LSMPA by the Mexican government [38].

3.2. Regional oceanographic conditions

The Revillagigedo Archipelago is located in an oceanic region between the subtropical gyres of the North and South Pacific, containing the eastern Pacific warm pool and the eastern terminus of the Pacific equatorial current system [45]. The islands lie in the transitory zone of the Northern Equatorial Current (NEC) and the California Current [46]. Over the course of an annual cycle, monthly SST values range from about 23.5 °C to 28.5 °C. Minimum SST is from January until June, reflecting the dominance of the California current in transporting cool waters from higher latitudes south. In June, the California Current weakens and the NEC, predominantly fed by the warm Northern Equatorial Counter Current (NECC), becomes the more dominant influence causing SST to increase [26].

The El Niño Southern Oscillation (ENSO) is the largest cause of interannual climate variability on earth [47]. This auto-oscillation involves the occurrence of two complementary phases, warm (El Niño) and cool (La Niña). El Niño, which is associated with elevated SST in the Central and Eastern equatorial Pacific, has had severe bleaching impacts on reef-building corals in the ETP [48]. Analysis of remotely sensed SST of the 1° grid box around each island in the Revillagigedo indicates that the maximum thermal anomaly during an El Niño event between 1982 and 2016 at Revillagigedo was about 2.4 °C. Fig. 2 demonstrates the temporal and magnitude differences between temperature anomalies between the Niño-3 index region (5°S-5°N, 150°W-90°W) and for the 1° grid box of each island representing the relative influence of El Niño on the SST at Revillagigedo. Regression analysis indicates that ENSO can explain 25%–38% of the annually averaged SST anomalies at the Revillagigedo Archipelago, noting that at seasonal and monthly timescales, this relationship weakens. In general, ENSO has more influence on the islands during the boreal autumn and winter than during the spring and summer, which can be attributed to the strength of El Niño that usually peaks during these periods [32].

The pycnocline in the ETP is shallow with a steep gradient [28]. This is caused primarily by the shallow and steep temperature gradient of the thermocline (1 °C every 10 m depth) [49]. Seasonal variations in the Inter Tropical Convergence Zone (ITCZ) translate into seasonal changes of the topography of the thermocline. At Revillagigedo, the thermocline is at its shallowest in September at around 25 m. This is caused by the northward migration of the ITCZ causing upwelling across the ETP and consequent shoaling of the thermocline. As the ITCZ moves south the thermocline deepens, reaching a maximum depth of 70 m between

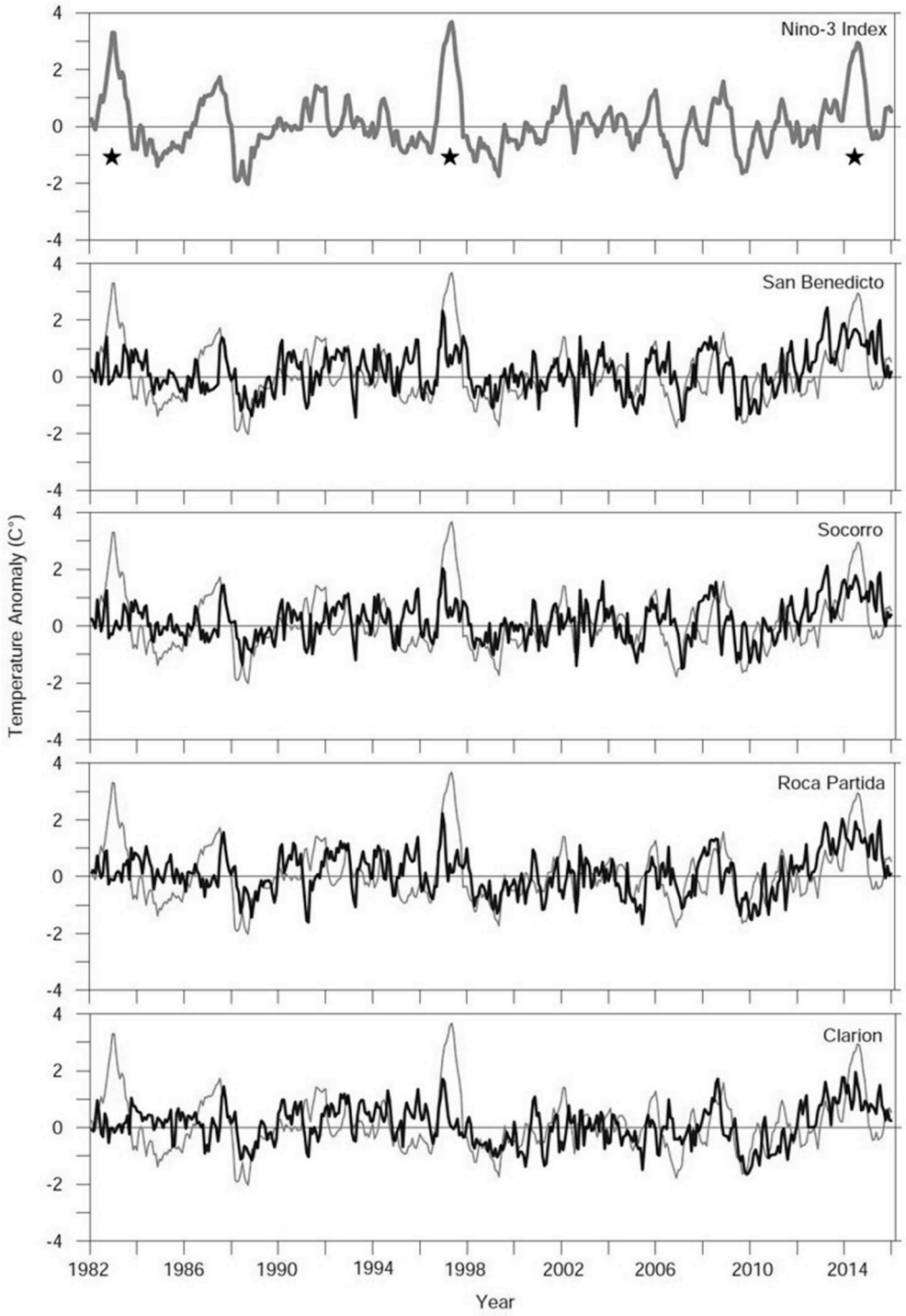

Fig. 2. Average monthly SST anomalies of the Niño-3 index region (top) compared with the average monthly SST anomalies of the 1° grid box containing each island in the Revillagigedo Archipelago from 1982 to 2016 (IGOSS Reyn_Smith OIv2). Stars indicate large El Niño events of 1982/83, 1997/98 and 2015/16. With exception of the top graph, the thick line represents the SST anomalies of the oceanic region around each island and the thin line the Niño-3 index region.

January and March. The top of the oxygen minimum layer is positioned between the pycnocline and subpycnocline waters between 60 m and 80 m water depth. In the ETP, the oxygen minimum layer is remarkable for its large size and degree of oxygen deficiency [50]. This can be attributed to a highly productive photosynthetic layer at the surface; the sharp and permanent pycnocline impeding the exchange of oxygen-rich water from the surface and the slow turn-over time of the subpycnocline waters [28].

3.3. Localised oceanographic conditions

Fig. 3 shows the temperature measurements for the recording periods of the *in situ* temperature loggers between May 2016 and March 2017. This period coincided with relatively neutral conditions in terms of the Niño-3 index of ENSO. Daily temperature variations are generally in the range of 2 °C–3 °C (maximum minus minimum) but notable features are the periods with high temperature variability, with the same days seeing a change of up to 7 °C. In other oceanic reef locations, such

temperature variability has been attributed to the occurrence of internal waves inducing episodic, short-duration upwelling 'events' of colder waters [51,52]. The upwelling is a result of a temperature-stratified water column being driven alternately up and down a slope by oscillating tidal currents. For a temperature record measured at a fixed depth, it may be expected to find temperature variations fluctuating with the same period as the dominant tidal flows. At the Revillagigedo Archipelago, there are likely to be complications to this simplified picture in that there may be local variations due to complex volcanic bathymetry, and local variations in the stratification (e.g. to greater mixing in shallow or more exposed sites). At the range of latitude of the Revillagigedo Archipelago, the dominant astronomical forcings of tidal elevations are the principal lunar (M2), principal solar (S2) and luni-solar diurnal (K1) constituents, which have periods of 12.42, 12.00 and 23.93 h respectively. The relative amplitudes of the celestial gravitational tidal forces are [M2:S2:K1] = [1 : 0.46: 0.36]. Correspondingly, between 2005 and 2007, an oceanographic buoy anchored approximately 700 m south of Socorro, recorded M2 and K1 tidal components at the surface in *u* and *v* ocean current data [30]. In addition to tidal current oscillations, strong wind events have a tendency to induce oscillatory currents in the ocean, so-called 'inertial oscillations', denoted by the Coriolis parameter (*f*). Inertial oscillations manifest as horizontal currents vectors rotating with a period dependent on latitude (varying from 12 h at the poles, to infinity at the equator). In theory, inertial oscillations can also induce cold upwelling in a similar manner to tidal oscillations. The inertial period varies between 35 and 40 h at 18°N to 19.5°N. There is an important distinction between the tidal and inertial periods. At this latitude, all the tidal periods mentioned above can create internal waves which are freely propagating, whilst at the inertial periods the energy in oscillations is not able to propagate from one place to another. In other words, at a given location any observed inertial currents must be locally generated, whilst internal waves of tidal frequency may either be locally or remotely generated. At the oceanographic buoy located 700 m south of Socorro, well defined spectral peaks for temperature and the *u* component of ocean current data were observed at the theoretical inertial oscillation of period 37.4 h [30].

The temperature spectra (Fig. 4) from all three HOBO logger sites reveal enhanced temperature variability centred around the M2 period, with this concentration of variance being more pronounced at San Benedicto and Roca Partida than Socorro. Without knowledge of the strength of vertical temperature gradients at any of the sites (i.e. temperature stratification) it is not possible to speculate on the amplitude of the internal waves causing these periodic temperature variations on the reefs. It is likely that M2 and S2 signals both contribute to the spectral rise seen around the semi-diurnal period. No particular signal is seen at the K1 period (not marked), unsurprising given that the forcing of K1 is less than 25% of M2+S2 combined.

Tropical cyclones have episodic effects on oceanographic conditions in the form of increased wind and wave energy, and cool SST anomalies [53]. The islands of Revillagigedo Archipelago have been impacted by over 100 storms since 1980 (within 200 km of an island; https://coast.noaa.gov/hurricanes). Cooling effects of up to 6 °C have been recorded in the wake of tropical cyclones, caused by the upwelling and mixing of cold subsurface waters [54]. Accordingly, the cooling impacts of the four tropical cyclones which reached within a 200 km radius of San Benedicto, Socorro and Roca Partida during 2016 are visible on the *in situ* temperature measurements (Fig. 3). Furthermore, spectral analysis shows a broad peak in spectral energy around the inertial period band (Fig. 4). This suggests that, in addition to the internal tidal effects, the frequent storms of the region are important in driving periodic temperature variations on the time scales of hours to days. The magnitudes of cooling impacts are likely to be related to the proximity and strength of each storm and the duration it has in the zone of influence of the island [53]. Tropical cyclones in this region typically occur between May and November, during the period of warmest SST.

3.4. Recent and predicted future changes in oceanographic conditions

Linear trend analysis of SST in the Revillagigedo Archipelago region indicates warming of 0.7 °C from 1880 to 2010 [31]. The increase is moderate compared to an overall warming trend of the 20th century in the ETP of 0.8–1.0 °C [55], although, patterns of warming in the ETP are spatially and temporally complex owing to heterogeneous and dynamic nature of ocean processes [56]. General Circulation Models (GCMs) used

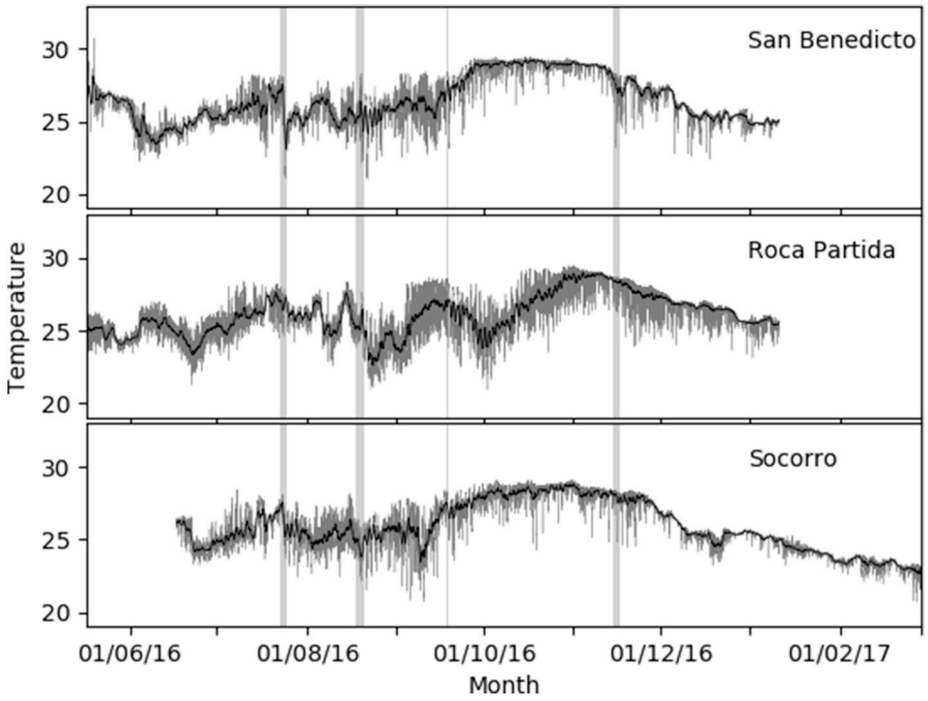

Fig. 3. In situ temperature data for San Benedicto (23 m water depth), Socorro (28 m) and Roca Partida (38 m): raw data (grey) taken at 13-min intervals and daily running average (black). Shaded vertical bars indicate the period tropical cyclones were within a 200 km radius of the islands.

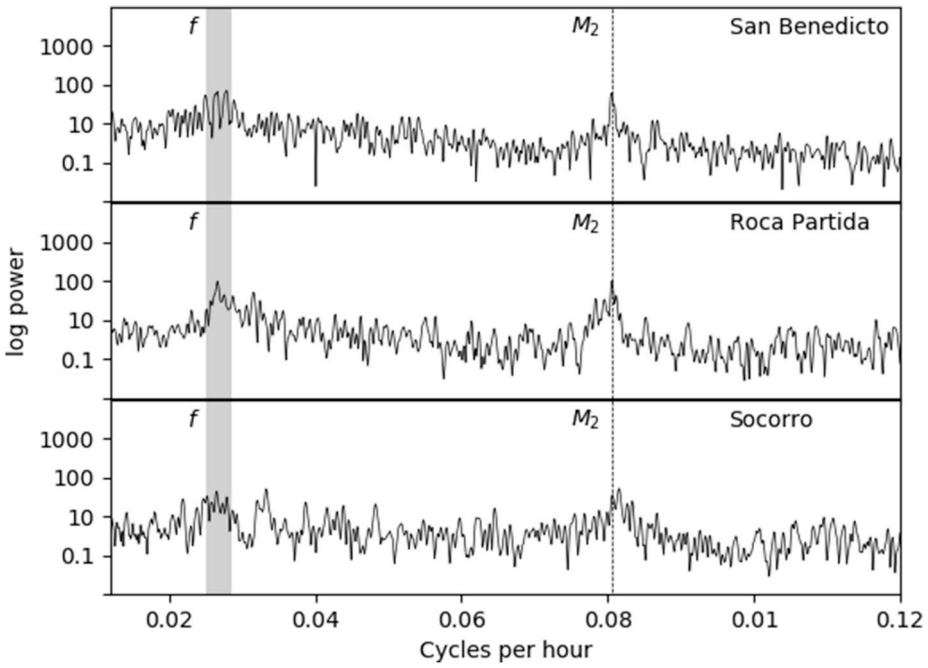

Fig. 4. Power spectra for 13-min interval temperature measurements recorded by *in situ* temperature loggers at the Revillagigedo Archipelago. Enhanced temperature variability can be seen around the principal lunar period (M_2; dashed line) and the inertial period at 18°N to 19.5°N (f; shaded vertical bar).

for climate prediction suggest that future anthropogenic warming is likely to be more intense in the equatorial region (~5°N to 5°S), than in the off-equatorial ETP regions [56]. However, projected increased rates of warming in the Eastern Pacific Warm Pool region [55] may influence the Revillagigedo Archipelago area on a seasonal basis, when the NEC is a dominant influence on oceanographic conditions.

Current generations of GCMs are unable to provide a consensus view on if and how interannual ENSO-variability will change in a warming world. Weakening trade winds and patterns of SST change may indicate a tendency of larger El Niño events, causing longer lasting SST anomalies with higher magnitudes in the ETP [57]. However, the extent that ENSO dynamics are impacted by climate change will be dependent on the relative balance of underlying climate processes and it is uncertain whether the expected changes in the amplifying and dampening processes of ENSO will partially cancel each other out [58].

3.5. Coral community and biogeography

Presently, 26 species of hermatypic corals have been recorded at the Revillagigedo Archipelago, with a possibility that the number is higher, since there is evidence of local hybridization of certain species [59,60]. Half of these species are endemic to ETP and one-third endemic to the Revillagigedo [42,60]. The coral community at the Revillagigedo Archipelago is slightly more species rich relative to other oceanic islands in the ETP such as Clipperton Island (21 species), Cocos Island (22 species) and the south and north Galapagos Islands (20 and 22 species), respectively [42] The dominant genera of corals in the ETP are *Pocillopora, Porites, Pavona* and *Psammocora* [42].

The coral community at the Revillagigedo Archipelago exists as isolated coral colonies and patchy fringing reefs, no larger than 1 ha in size [62]. In general, accumulations of reef framework are located at 4 m–8 m water depth. Below 15 m only isolated coral colonies and coral rubble exists [63] The principal areas of reef in the Revillagigedo Archipelago are *Pocillopora*-dominated fringing reefs and large coral heads of *Porites lobata* (up to 3.5 m height and 4 m in circumference) located in protected bays on the south and west coast of Socorro and Clarion Islands [64]. These reefs demonstrate clear zonation, dominated by *Pocillopora* in water less than 8 m water depth and an increasing abundance of *Porites* and *Pavona* from 8 m to 30 m. The island of San Benedicto hosts only small areas of fringing reef and isolated coral colonies [63]. On Roca Partida, the lack of horizontal rocky substrate prevents the accumulation of a reef framework. *Pocillopora* coral colonies grow on the small ledges [64], and the vertical sides have areas with high coverage of encrusting coral (Carter, personal observation).

The oceanic region of ETP represents an isolated biogeographic region, separated from the Caribbean Sea since the closure of the Central American land bridge (3.4–4 million years ago) and from the central and western Pacific by a 4000–7000 km expanse of open water, known the Ekman Barrier [65,66]. The highly dynamic current system causes marked spatial and temporal variability in larval transport and connectivity [67]. Relative isolation has caused high levels of endemism, but there is still evidence of a connection with the central and western Pacific with the presence of many of the same species [62], indicating that marine organisms are able to traverse the Ekman barrier using the Northern Equatorial Counter Current (NECC) [68]. This is supported by a mid-ocean planktonic survey which revealed the presence of numerous indo-Pacific littoral invertebrates in the ETP [67]. During El Niño events the speed of the NECC increases greatly. This has been proposed as a key mechanism for transportation of species from the central Pacific to the ETP, as it may reduce larval transit times to durations less than the larval duration of some coral species [62,69]. Migration of species from the ETP to the central and western Pacific has also been documented, with larval dispersal westwards enabled by the Northern Equatorial Current (NEC). For example, two *Pocillopora* sp. colonies of 2–3 years age attached to pumice, likely to have drifted from the Revillagigedo Archipelago, were recovered in the Hawaiian Islands [70]. Studies have suggested that the Revillagigedo Archipelago plays a significant biogeographic role in the ETP, acting as a steppingstone for immigrant species from the Indo-Pacific [59,68] and demonstrating connectivity with the distinct northern and southern coral communities located north of 24°N and south of 18°N in the Mexican Pacific [71]. Strong faunal similarities and a number of shared endemic species indicate significant connectivity with Clipperton Atoll [60] and coral species presence-absence classification indicates a distinctly connected northern coral province in the ETP comprised of mainland Mexico and the Revillagigedo Archipelago [72].

3.6. Coral bleaching

Coral bleaching events at the Revillagigedo Archipelago have not been well documented. This is attributable to the remoteness of the islands and the difficulty of accessing them during tropical cyclone season, which occurs during the warmest months of the year when bleaching is most likely to occur. The ability to estimate the severity of historic bleaching events remotely is made possible through the rapid synoptic reporting of SST by satellites. However, as it has been demonstrated in this study, subsurface temperatures of the waters surrounding the islands of the Revillagigedo Archipelago are subject to high frequency temperature variability. Subsurface temperature fluctuations which occur on the timescale of hours to days are likely to influence the severity of coral bleaching but will not be recorded by satellite SST measurements [73]. Therefore, satellite measurements may overestimate the severity of bleaching impacts. Furthermore, severity of bleaching is not solely reliant on thermal stress but also on an array of other factors influencing the corals including different physiological and genetic properties of coral hosts and symbionts and differences in the environmental history [48,74].

The 2015–2016 El Niño is one the strongest El Niño events on record, associated with high SST anomalies in the ETP [75]. A calculation of the DHW from this period at the islands of Socorro, San Benedicto and Roca Partida, indicates DHW values of >8°C-weeks, a level of thermal stress usually associated with widespread coral bleaching and mortality [34]. In November 2015, opportunistic field observations during SCUBA dives at Socorro and San Benedicto indicate coral bleaching ranged from zero to 70% on individual coral colonies and reef areas. In reef areas, bleaching was observed to be more severe on *Pocillopora* than on other dominant species, *Porites* and *Pavona*. No coral bleaching was observed during SCUBA dives at Roca Partida. On dives in November 2016 at Socorro and San Benedicto, no bleaching was observed and the corals appeared to have recovered from the previous years' bleaching event with little evidence of mortality (Ketchum, personal observation). Together, these observations indicate that coral bleaching and mortality at the Revillagigedo Archipelago was less severe than would have been anticipated from the satellite-derived DHW predictions.

4. Is the Revillagigedo Archipelago a potential coral refugia?

Building on the review of oceanographic conditions and coral communities in the previous section, and on the essential characteristics of refugia (summarised in the Introduction and detailed in articles [8–11]), the following section discusses the features of the Revillagigedo that are indicative of a potential coral refugia.

4.1. Regional oceanographic conditions relevant to refugia

From 1880 to 2010, the Revillagigedo Archipelago experienced a moderate increase in SST of 0.7 °C and from 1982 to 2017 a maximum regional thermal anomaly of 2.4 °C associated with El Niño event. This is likely to have caused relatively less stress for the coral community at the Revillagigedo Archipelago compared to temperature related stress experienced in coral regions at lower latitudes in the ETP which have had a greater increase in SST and experienced greater ENSO related thermal anomalies (e.g. 6° [76]). Furthermore, in this review we have demonstrated that it is likely that the coral community at the Revillagigedo Archipelago regularly experience temperature variability of greater than 2.4 °C and therefore are likely to have greater resilience to temperature related stress [20]. Low incidence of mortality observed following coral bleaching at the Revillagigedo Archipelago supports this theory. If favourable temperature conditions in the Revillagigedo Archipelago are maintained, there could be opportunity for it to serve as a safe haven for *ex situ* tropical species that migrate polewards as conditions in equatorial latitudes become unfavourable [77,78]. However, it is recognised that the long-term effectiveness of refugia is uncertain and will be determined by spatially complex ocean warming trends in the ETP and the effect of a warming ocean on the dynamics of El Niño events.

4.2. Influence of local oceanographic conditions on potential refugia status

In situ temperature measurements taken at islands in the Revillagigedo Archipelago indicate the presence of high frequency temperature variability. These are attributed to internal waves caused by tidally driven oscillation of the highly-stratified water column and intermittent vertical mixing caused by tropical cyclones. The loggers that recorded the internal waves were placed between 23 and 38 m, deeper than much of the coral community. Indeed, the restriction of the coral community to relatively shallow water depths may be partly related to the level of exposure to the internal wave regime [79]. Nonetheless, based on evidence indicating the influence of internal waves on coral communities elsewhere [51,80,81] and on personal scuba-diver observation of large and rapid temperature changes at coral locations at Revillagigedo, it is hypothesised that the corals at Revillagigedo are regularly impacted by temperature fluctuations caused by internal waves.

Site specific studies have highlighted that temperature fluctuations within tidal timescales can improve the tolerance of corals to thermal stress [21,81]. Furthermore, a recent review found high-frequency temperature variability was the most influential factor in predicting bleaching prevalence and was found to reduce the odds of severe bleaching [20]. These studies indicate that thermal stress caused by high frequency temperature variability encourages adaptation or acclimation of corals to higher thermal tolerance while occurring over durations short enough to avoid long-term detrimental impacts. Adaptation for greater thermal tolerance in corals can occur through natural selection of more heat-tolerant lineages of the coral animal or algal symbiont [82,83]. The genotypic adaptation of corals over evolutionary timescales is unlikely to occur at a rate concurrent with anthropogenic climate change [84]. However, zooxanthellae symbionts have much shorter generation times and there are certain genotypes of the symbiont which exhibit more heat tolerance than others [85]. After exposure to thermal stress, there is evidence that corals have adapted to higher temperatures by acquiring more thermally tolerant symbionts through symbiont ‘shuffling’ [86]. Evidence of increased thermal tolerance of coral communities caused by symbiont shuffling has been recorded across reefs in the ETP following periods of thermal stress and bleaching [87,88]. The extent to which heat-tolerant symbionts will protect multi-species coral assemblages remains uncertain as constraints and trade-offs between phenotypic plasticity and physiological performance are likely to limit the phenotypic responses of some coral species [89]. Likewise, corals may acclimate to thermal stress using their existing genomic repertoire such as through the release of antioxidant enzymes and production of heat shock proteins [83]. However, this will be dependent on the physiological and genomic characteristics of the coral species [90].

Exposure to internal waves not only implies a cooling effect, but also enhanced flushing and water movement of water masses surrounding the corals [91]. This periodic exchange of water masses may be important in preventing excessive build-up of detrimental photosynthetic products, produced in the stress reaction of the algal symbiont and further mitigate the deleterious impacts of bleaching [92,93]. Additionally, the intrusion of subthermocline nutrient-rich waters can increase the supply of heterotrophic food for corals [21]. Under normal conditions corals derive much of their energy from zooxanthellae. When zooxanthellae are expelled during bleaching, some coral species can increase carnivory to meet daily metabolic energy requirements and reducing mortality from bleaching [94]. *Pocillopora,* the dominant reef building coral at Revillagigedo, has been shown to be capable of this form compensatory trophic switching when under stressed conditions [95].

In situ temperature measurements indicate that at Revillagigedo,

internal waves occur throughout the year including during periods of the warmest SST. Therefore, internal waves may provide intermittent cooling, which although short-lived, could also reduce overall heat stress during these periods [73]. The nature of tidal driven internal waves is influenced by variations in the stratification of the water column [96]. Over longer timescales, phenomena including El Niño and increasing ocean temperatures may cause variation in the structure of the water column which in turn may impact the nature and frequency of internal waves.

The Revillagigedo Archipelago LSMPA region experiences 3 to 4 tropical cyclones per year. *In situ* sea temperature measurements demonstrate the cooling effect these cyclones have on the sea surface temperature, caused by the entrainment and upwelling of cool subsurface water [97]. Satellite observation and *in situ* measurement have shown these cooling effects can last for days or weeks [54]. Although destructive wave action caused by the cyclones can potentially damage reefs (e.g. large coral rubble areas observed at Clarion and Socorro), there is evidence that if the cooling effect of a cyclone coincides spatially and temporally with periods of thermal stress, they can reduce the severity and duration of coral bleaching [98]. Moreover, tropical cyclones do not have to coincide with thermal stress periods to be beneficial, as it is possible their occurrence alone may disrupt the seasonal SST warming cycle, preventing or reducing the temporal period over which the thermal threshold is exceeded [53]. It is acknowledged that caution must be used when attributing intermittent phenomena to climate refugia as they cannot promise long-term protection against changing climate conditions [8]. Furthermore, under climate change the frequency and intensity of tropical cyclones may be altered [99]. However, currently at Revillagigedo, the seasonal cooling impact of recurrent tropical cyclones during the period of warmest SST play a large role in temperature conditions experienced in the region and therefore are considered a potential feature of refugia conditions.

4.3. Features of the coral community and biogeography relevant to refugia

The characteristics of the coral community are likely to be correlated to their resilience to environmental change [11]. The coral community at the Revillagigedo Archipelago hosts one of the most species rich coral ecosystems in the ETP with many endemic species. In terrestrial refugia, rich species diversity and relatively large amounts of endemism are reported to indicate past climatic stability [100]. Furthermore, species diversity is an important characteristic of resilient ecosystems as it increases the chances of ecological redundancy to ensure the maintenance of ecological processes [24]. Dominant reef-building species such as *Pocillopora* have exhibited self-recruitment through asexual propagation, but also the ability to persist as planktonic larvae for weeks to months, dispersing over thousands of kilometres [101]. Self-recruitment will become increasingly important to the maintenance of populations if numbers of larvae from other region decrease because of reduction at the source or changing oceanographic patterns. On the other hand, high connectivity with other regions may also aid future adaptation if the larvae originate from corals that have demonstrated high resilience to changing environmental conditions [102]. At Revillagigedo, significant levels of self-recruitment indicated by the coral biogeography and high levels of endemism suggest the coral populations could persist if oceanographic barriers caused by changing climate conditions reduce the arrival of *ex situ* coral larvae [23]. However, connectivity of coral communities has been identified as a key criterion for refugia in some coral ecosystems [8]. Indeed, according to Keppell [5], an area of climate refugia should assist with the expansion of species range, subsequent to their retraction to a limited spatial extent owing to unfavourable environmental conditions. At the Revillagigedo Archipelago, larval connectivity has been reported with the Central Pacific, other oceanic islands in the ETP and with the coastal regions of mainland North and Central America [68,103]. On a short-term timescale, maintenance of a coral populations through long-distance dispersal is unlikely [104], however, on a centennial to millennial time-frame long-distance connectivity may assist with the migration and expansion of persistent coral species from the Revillagigedo Archipelago to other regions [105].

5. Management perspective and implications

5.1. Reduction or absence of secondary stressors

If the oceanographic and ecological conditions associated with refugia occur in an area of high human impact, stressors associated with human activities may compromise the ability for these locations to accommodate healthy and persistent coral ecosystems [24]. For example, pressures such as overfishing and poor water quality have been found to decrease reef resilience to the impacts of increased ocean temperatures [106,107]. The Revillagigedo Archipelago has relatively limited exposure to these threats as it is a no-take marine reserve which is undeveloped and uninhabited except for the infrastructure and residents of naval bases on Socorro and Clarion. Other frequent human activities, related to dive tourism operating seven months of the year, are highly regulated and cause little disturbance to the coral ecosystem. Additionally, the large size of the MPA (148,800 km^2) and permanent enforcement presence (associated with the naval bases) may contribute to the effectiveness of the MPA in protecting a diverse range of species and ecosystem processes [108,109]. The presence of diverse species and ecosystem processes supports existence of complex trophic interactions between benthic, reef fish and pelagic communities which can improve coral reef resilience [110]. The capacity of refugia at the Revillagigedo Archipelago will be largely determined by the oceanographic conditions and characteristics of coral community, nonetheless, the relatively limited presence of anthropogenic stressors will enable the full potential of refugia to be fulfilled.

5.2. Management and learning opportunities

In recent years, identification of refugia habitats using ecological and climate data, and the incorporation of refugia in conservation planning, have been widely adopted in terrestrial environments [111–113]. Yet, despite a significant body of work to define refugia for corals, there is little evidence of the concept being considered in MPA management decisions. Utilising available data and knowledge it can be inferred that certain oceanographic and ecological conditions at the Revillagigedo Archipelago LSMPA are characteristic of refugia. These characteristics could support the persistence of corals through climate change, as well as the health of the wider reef ecosystem and the pelagic organisms which utilise the reef at critical life stages. The remote setting, large size and current management measures of the Revillagigedo Archipelago LSMPA minimises risks from direct anthropogenic stressors in the MPA, and to some extent, indirect spill-over effects from anthropogenic activities occurring outside the boundary of the MPA. Therefore, the Revillagigedo Archipelago LSMPA is in a fortunate position where restrictive management interventions are not currently required to maintain the health and thus, the capacity of refugia, of the coral ecosystem.

Although the concept of climate refugia for coral reefs has been discussed for over 2 decades [114], there is still a paucity of direct evidence of which environmental and ecological conditions are optimal. Therefore, there is both a need and an opportunity to recognise the Revillagigedo Archipelago as a globally-significant sentinel (research) site [116], in which the conditions of refugia can be empirically investigated. Through high resolution and long-term monitoring of the oceanographic and climate conditions, and of the coral and associated marine ecosystems, the impacts of climate change on the corals may be quantified, and the specific oceanographic and ecological attributes of refugia established. By using this biogeographically-important location, removed from direct anthropogenic stressors such as land-derived

pollution, over-fishing or other forms of disturbance and extraction, climate-specific impacts on the coral ecosystem may be more confidently isolated. This anticipatory and hands-on learning approach to defining climate refugia may then help inform the designation of coral-relevant MPAs elsewhere, and help guide management decisions on where reducing direct impacts may pay the greatest long-term conservation dividends. This opportunity is especially timely given the recent and ongoing rapid expansion of MPAs with coral reefs as whole or part of their underlying rationale [115].

6. Conclusion

Given the severity of coral bleaching and mortality caused by ocean warming, it is important our current knowledge of climate refugia is utilised to identify refugia locations. A review of current knowledge of the oceanographic conditions and coral community at The Revillagigedo Archipelago indicates it has characteristics of refugia. These characteristics are:

- A moderate ocean warming trend and weaker El Niño associated thermal anomalies than other regions of the ETP;
- Frequent high-frequency temperature variability caused by internal waves promoting coral resilience to temperature stress;
- Intermittent high-frequency temperature variability caused by tropical cyclones promoting coral resilience and having a cooling impact on SST during the warmest period of the year;
- A coral population with rich species diversity (relative to coral populations in the ETP) and significant self-recruitment to maintain *in situ* coral populations if the arrival of *ex situ* larvae decreases;
- A coral population with high connectivity which could support the expansion of persistent coral species over centennial to millennial time-frames; and
- Limited impact of direct anthropogenic stressors.

We propose long-term, high-resolution monitoring of the oceanographic conditions and coral ecosystem at the Revillagigedo Archipelago LSMPA should be undertaken to assess the ecosystem response to changing climate. This can provide scope for the Revillagigedo Archipelago to serve as a sentinel site to understand global level changes without the impact of secondary anthropogenic stressors and provide a learning opportunity to support the identification of refugia in other locations. While it is important to acknowledge the uncertainties of future climate change and its impact on the processes and biological responses underlying coral reef refugia, identification of refugia sites will highlight conservation priorities that will support the persistence of coral ecosystems in the future.

Declaration of competing interest

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CRediT authorship contribution statement

Amber L. Carter: Conceptualization, Investigation, Methodology, Formal analysis, Writing - original draft, Visualization, Funding acquisition. **A. Meriwether W. Wilson:** Writing - original draft. **Maximiliano Bello:** Funding acquisition, Conceptualization. **E. Mauricio Hoyos-Padilla:** Resources, Writing - review & editing. **Mark E. Inall:** Writing - review & editing, Writing - original draft. **James T. Ketchum:** Resources, Writing - review & editing. **Andrew Schurer:** Formal analysis, Visualization. **Alexander W. Tudhope:** Conceptualization, Writing - original draft, Funding acquisition, Supervision.

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Appendix A. Supplementary data

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